

A COMPARATIVE MORPHOLOGICAL STUDY OF THE HIND WING
VENATION OF THE ORDER COLEOPTERA, PART I.

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ABSTRACT—A comparative morphological study of the wing venation of Coleoptera determined that the coleopterous venation has a close affinity to the venational pattern exhibited by the suborder Megaloptera of the order Neuroptera. In addition, the available fossil record revealed that no single described wing possessed the composition necessary to serve as a coleopterous ancestral form. Therefore the alternative was the selection of a pattern which would serve as a guide in determining the line of development leading to both Coleoptera and Megaloptera. The order selected was the fossil order Protorthoptera.

From a study of the Megaloptera, Protorthoptera, Lepidoptera and the families of Coleoptera, a comparative coleopterous-megalopterous pattern was constructed, the composition of which included a pectinate radial pattern, an anal lobe consisting of a postcubital vein, a lack of any anal cross-vein pattern, and the establishment of a single anal vein which has undergone branching. Such a pattern served as a basis for comparison of Coleoptera to Megaloptera as well as the various patterns exhibited by the families within the Coleoptera.

Early investigations of insect wing venation were based on comparative morphology with an attempt to establish a uniform terminology of wing venation throughout the different orders of winged insects.

Many early workers (Hagen, 1870; Adolph, 1879; Redtenbacher, 1886) attempted to homologize the wing veins of the various orders of insects and developed the current system of venational nomenclature. However, due to the inability of establishing a uniform system of terminology as well as the lack of sufficient fossil evidence, comparative studies were relegated a secondary role in favor of the ontogenetic study of wing venational homology as proposed by Comstock and Needham (1898a, 1898b and 1899, and Comstock 1918).

Objections to this ontogenetic method of determining venational homologies were raised by Tillyard (1928), Martynov (1924) and Carpenter (1966), all of whom believed that certain facts, established as the result of applying the ontogenetic approach, were in conflict with the fossil record. Thus there developed a new school of thought based upon the concept that the true nature of venational homologies was dependent upon the study of the fossil record.

Recent investigators, such as Holdsworth (1940, 1941), Smart (1956), Whitten (1962) and Leston (1962), conducted histological studies concerning the nature of the development of nymphal wing pads, tracheae and veins. From these investigations, it was concluded that tracheation could not be taken as fundamental in determining the homologies of the insect wing veins.

An approach similar to the one used in the present paper was conducted by Adams (1958). In this study he used both comparative morphology and paleoentomological evidence in support of the parallel venational pattern exhibited by the present-day suborder Megaloptera and the fossil family Lemmatophoridae.

Lameere (1922), Snodgrass (1935), Carpenter (1943a, 1943b, 1966) and many others have proposed various theories which in part have helped to develop some of the venational nomenclature presently in use.

Although the ontogenetic method is not considered fundamental, many of the conclusions reached by Comstock and Needham as a result of their comparative studies provided a basic foundation for solving the evolutionary venational affinities of the alate insect orders. We realize that the last word in solving problems concerning the homologies of insect wing venation rests with the discovery of new fossil insect records. Wherein the insect fossil record is incomplete, the solution to venational problems depends largely on studies of comparative morphology involving present-day insect groups.

The order Coleoptera is one such insect group, which was regarded by Comstock as an order in which the veins of the wings preceded their tracheation. Therefore the venation of such a highly modified pattern did not lend itself readily to interpretation but required evidence of a more extensive nature.

Although the present paper follows the recent evidence which considers tracheation as an inaccurate guide to determining wing venational homologies, much of the work conducted by Forbes (1922) was based upon comparative studies and is regarded as fundamental. Therefore the present study is a modification and expansion of the Forbes system as a result of evidence accumulated from an investigation of the fossil records, a more extensive study involving a comparative morphology of the families of Coleoptera, and wing venational concepts proposed by investigators since Forbes.

In order to consider such a proposal, it is necessary to provide a basis upon which a comparison can be drawn between the Coleoptera and on the basis of other characters, a closely related present-day order of insects. It has been determined by several workers that the larval and adult features of Coleoptera share many characteristics found in the order Neuroptera. Forbes concluded that the coleop-

terous wing venation is based upon the same fundamental plan as that of Neuroptera. Although Forbes recognized this affinity, he did not attempt to construct his hypothetical coleopterous wing from any other than the wings within the order Coleoptera itself.

Parallel evidence in regard to paleoentomological affinities is based upon a study of the Lemmatophoridae, which possesses both a well developed anal lobe and anal pattern. The anal pattern exhibited by the Lemmatophoridae is interpreted as having much in common with both Megaloptera and Neuroptera.

Therefore, in view of the converging evidence accumulated, this study will:

1. Illustrate that Coleoptera, although exhibiting an unusual type of venational pattern, shares a pattern common to all other alate insect orders.
2. Compare the coleopterous wing venation to that of the neuropteroid group, the suborder Megaloptera.
3. Demonstrate that such a venational pattern as seen in the Lemmatophoridae shares much in common with both the Coleoptera and the Megaloptera.
4. Conduct a comparative study of the individual coleopterous families, as well as their relationship to the comparative coleopteran venational pattern.

MATERIALS AND METHODS

Many of the wings selected were drawn from slides of the various families included in the excellent and extensive collection of Dr. Edwin W. King, Professor of Entomology, Clemson University. Much of the Scarabaeidae analysis was the result of the particularly large series which is a part of this collection. Certain families or species of a particular family not available, required the use of the following technique for removal of the wing.

1. Relaxation of the specimen was accomplished either by leaving it in a relaxing jar for several days or more rapidly by placing the specimen in hot water for a few minutes.
2. Since a beetle is pinned through the right elytron, the left elytron was raised and with a pair of fine forceps the left wing was removed. This procedure involved grasping at the base and carefully removing the hind wing including the basal sclerites. Care was taken to prevent tearing either the wing or the thorax.
3. The wing was placed in 70% ethanol and then carefully unfolded and spread by means of blunt needles. Following this the wing was transferred to absolute alcohol for about 2 minutes. Then the wing was washed briefly in xylene and placed on a slide containing a drop of synthetic mounting medium, the basal sclerites were cut away and final spreading and orientation of the wing was made. A cover slip was placed in position, after

which a gentle pressure was applied to further spread the wing and remove excessive mounting medium.

4. If spreading proved difficult, the wing was transferred from 70% alcohol directly into hot water which aided in the unfolding.

In order to obtain a constant size and proportion, the illustrations were drawn with the aid of a modified microprojector Ken-A-Vision Model No. L 2. Drawings are original unless otherwise designated.

RESULTS AND DISCUSSION

In meeting the objectives set forth, certain assumptions were necessary. They are:

1. The wing venation of Insecta is arranged on a common plan.
2. The earliest venation was simple in pattern as proposed by Comstock (1899).
3. A parallel venational pattern exists in both present-day forms as well as fossil forms, which serves as a guide to the homology of the veins in Coleoptera.

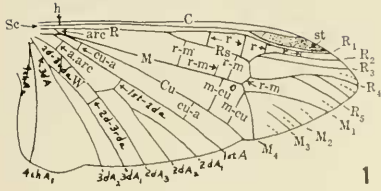
In order to gain an understanding of the unusual type of venation seen in Coleoptera, it was necessary first to conduct a comparative study of selected generalized wings from the families of Coleoptera. The selection of the generalized family venational pattern was based upon the most complete and stable venation available. The number of genera and species studied per family varied considerably ranging from large series as represented by the Buprestidae and Cerambycidae investigations of Good (1925, 1929), to that of a single specimen. The venational pattern of a single specimen is not necessarily representative of the generalized venation of a given family.

The hypothetical coleopterous wing of Forbes (fig. 1) was based upon three families: Cupedidae, Cembrionidae, and Hydrophilidae. A more detailed analysis involved application of information received from such additional families as Scarabaeidae, Dermestidae, Dytiscidae and Cerambycidae.

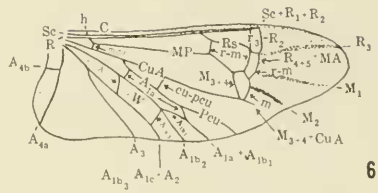
Since Neuroptera is considered closest to the Coleoptera, further comparative studies were conducted within this order. The principal character sought was the possession of an anal lobe with venation enough to compare to the Coleoptera. Such a requirement was found in the family Corydalidae, suborder Megaloptera. Examination of

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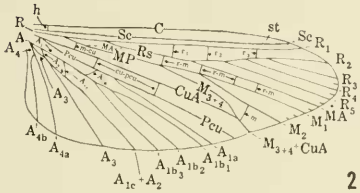
Fig. 1, Coleopterous hypothetical wing of Forbes; redrawn from Forbes, 1922. 2, Comparative coleopterous-megalopterous venational pattern. 3, *Aphodius denticulatus* Hald. (Scarabaeidae). 4, *Paraprisca fragilis* (Sellards) (Protoperlaria; Lemmatophoridae); after Tillyard, 1928. 5, *Scaptoleus lecontei* (Sallé)



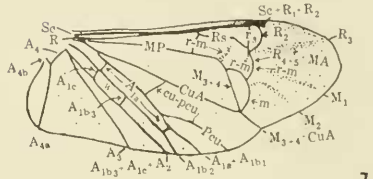
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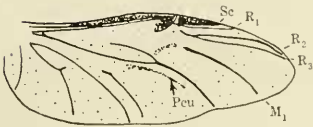
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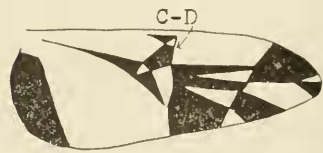
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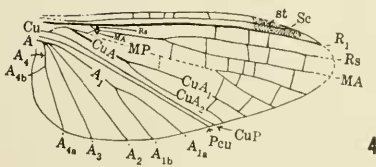
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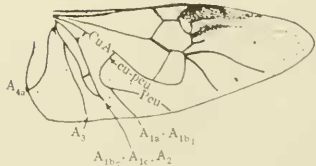
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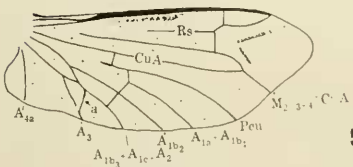
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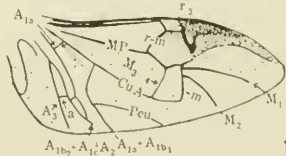
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(Cebionidae), pattern of individual variation in the species. 6, *Priacma serrata* (Lec.) (Cupedidae). 7, *Cupes concolor* Westw. (Cupedidae). 8, *Harpalus caliginosus* (Fab.) (Carabidae); folding pattern. 9, *Dineutus assimilis* (Kby.) (Gyrinidae). 10, *Dineutus ciliatus* (Forsberg) (Gyrinidae).

the fossil records revealed that the fossil family Lemmatophoridae possessed a comparable venational pattern.

In addition to the importance of the comparison in relation to the anal venation, the family Corydalidae also serves as a basis for an understanding of the preanal pattern. Included as supportive evidence in establishing the coleopterous preanal venation are some selected parallel patterns exhibited by Sialidae and Lepidoptera.

It is necessary, before entering into a discussion involving the trends of specialization within the Coleoptera, to analyze each particular vein and cross-vein which enters into the synthesis of the proposed comparative coleopterous-megalopterous venational pattern (See Plate 1 and fig. 2).

In the order of appearance from anterior to posterior the longitudinal veins are as follows:

Costa (C)—This is the very anterior marginal vein, considered present throughout the Coleoptera.

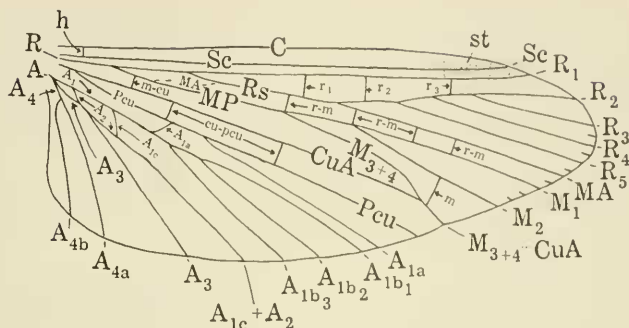
Subcosta (Sc)—This second longitudinal vein is in close proximity to the radius. The condition of this vein will be discussed in its relationship to radius.

Radius (R)—The radius runs parallel to the subcosta and in comparison to the Scarabacidae pattern does not appear to fuse at the apex (fig. 3). When compared to the fossil hind wing of *Parapresia fragilis* (Sellards), family Lemmatophoridae (fig. 4), the subcosta also is distinct apically with that of the radius, and in turn passes through a stigmatic area. Therefore, by comparison, it appears that the condition, as noted in the Lemmatophoridae, is paralleled in the Coleoptera and indicates a more generalized condition than occurs in present-day Megaloptera.

Radial Sector (Rs)—In the Coleoptera, the principal vein branching from radius generally atrophies at the base forming what often is referred to as a radial recurrent (Rr). The radial sector, as interpreted by Forbes (1922), branches from the radius in the same manner as would be found in the Cupedidae.

It appears as noted in the Cebriionidae, that the branching of the radial sector could be interpreted as arising more basally (fig. 5). This would be more in keeping with the pattern of the radial sector and its relationship to the anterior media formed in both the Corydalidae and Lemmatophoridae.

From a comparative study of the Adephaga, Cupedidae, Scarabacidae and Hydrophilidae it becomes apparent that the factor, which greatly influenced the unusual configuration of the radial sector as well as the apical venation, is that of folding. Accompanying this unusual configuration is either complete absence of part of the venational pattern or the presence of sclerotized venational traces. There-



Abbreviations Used

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| C - Costa | h - humeral |
| Sc - Subcosta | r - radial cross-vein |
| R - Radius | r-m - radio-medial cross-vein |
| Rs - Radial sector | m - medial cross-vein |
| M - Media | m-cu - medio-cubital cross-vein |
| MA - Anterior media | cu-pcu - cubito-postcubital cross-vein |
| MP - Posterior media | st - Pterostigma |
| CuA - Anterior cubitus | a - Accessory longitudinal vein |
| CuP - Posterior cubitus | W ₁ - Primary wedge cell |
| Pcu - Postcubitus | W ₂ - Secondary wedge cell |
| A - Anal | W ₃ - Tertiary wedge cell |
| A ₁ , A ₂ , A ₃ , A ₄ - Primary anal branches | |
| A _{1a} , A _{1b} , A _{1c} , A _{4a} , A _{4b} - Secondary anal branches | |
| A _{1b1} , A _{1b2} , A _{1b3} - Tertiary anal branches | |

Plate I. Comparative Coleopterous-Megalopterous venational pattern.

fore, as a result of a sharing of other parallel venational affinities, the coleopterous apical venation has much in common with the basic pectinate nature of the radial pattern as noted in the Corydalidae. Although based upon the same fundamental plan, it becomes necessary

from a study of the families in both the Cupedidae-Adephaga series, as well as the Polyphaga series, to construct separate comparative illustrations in order to explain the different lines of specialization along which the apical patterns developed.

In the Cupedidae-Adephaga (fig. 6-18) emphasis was placed upon the fusion of radial sector with radius. In turn, as a result of folding similar to the generalized condition of the Cupedidae-Adephaga line (fig. 8), a C-D fold (Forbes, 1926) slightly alters either the radial sector in its path, as in the Cupedidae (fig. 6-7) or completely interrupts the radial sector as appears in most of the Adephaga (fig. 11-18). Most of the apical venational pattern is lost, leaving only a trace of the principal veins in the radial area.

The remaining apical pattern (fig. 19-20) consists of a third radial cross-vein (r_3) distal to the C-D fold. In addition R_1 fuses distally a short distance with the fused vein R_{4+5} plus anterior media (MA). R_3 then becomes a prominent vein running nearly to the margin of the wing. There remains in the Adephaga only a spur of what is believed to be the fused branches $R_{4+5} + MA$. Included is a series of hypothetical stages (fig. 21-24) suggesting the possible manner in which folding has influenced a basic pectinate pattern to produce the type of apical venation exhibited by the Cupedidae-Adephaga series.

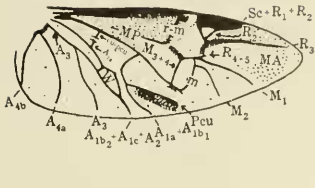
Although the Hydrophilidae (fig. 26) retain what appears to be a complete apical venation, a further study of the Scarabaeidae series proves instructive in interpreting the fusion of the branches of radial sector.

The configuration of the polyphagan pattern (fig. 27-29) is interpreted as a forcing of the branches of the radial sector to separate proximal to the C-D fold (fig. 30). This involves the forcing of R_2 and R_3 toward the anterior margin at a point distal to the second radial cross-vein. In the same respect R_4 , R_5 , and MA are forced toward the medial branch. There is the additional fusion basally of R_2 with R_3 as well as R_4 with R_5 . R_{4+5} is accompanied also by fusion with MA.

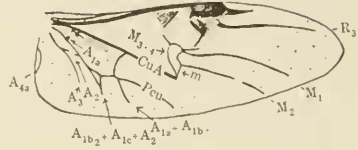
As a result of the comparison of the Hydrophilidae to that of the Corydalidae, it is entirely possible that the apical pattern consists of several accessory branches. This is indicated in the comparative

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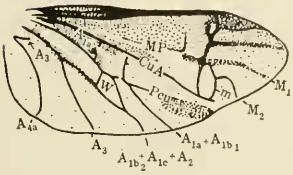
Fig. 11, *Agabus lugens* (Lec.) (Dytiscidae). 12, *Amphizoa insolens* LeC. (Amphizoidae). 13, *Hygrobia hermanni* (Fab.) (Hygrobiidae). 14, *Hydrocanthus iricolor* Say (Noteridae). 15, *Peltodytes muticus* (LeC.) (Halipidae). 16, *Rhysodes* sp. (Rhysodidae). 17, *Calosoma sycophanta* L. (Carabidae). 18, *Cicindela sexguttata* Fab. (Cicindelidae). 19, *Gyrinus fraternus* Coup. (Gyrinidae). 20, *Cicindela sexguttata* Fab. (Cicindelidae).



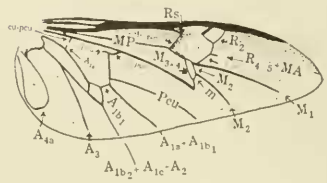
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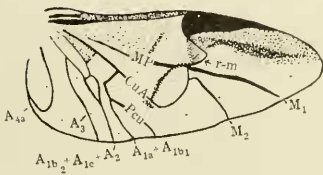
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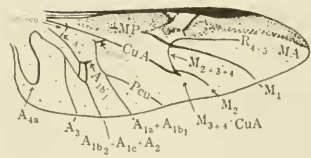
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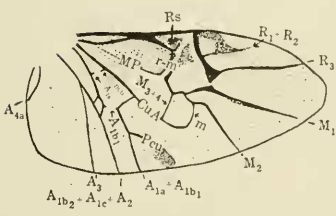
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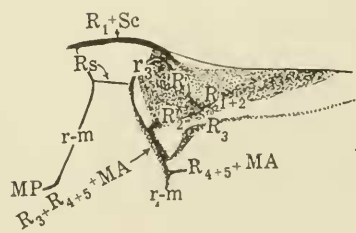
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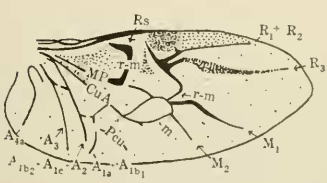
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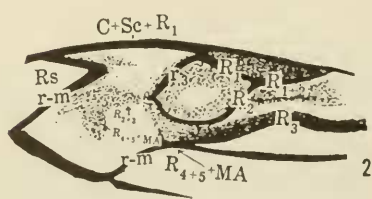
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patterns by a dash placed between two main branches. Since accessory veins are considered a part of the original pattern and due to the incomplete nature of the coleopterous apical venation, only an approximation can be given to the amount of accessory venation attributed to any primary branch (i.e. Hydrophilidae).

Anterior Media (MA)—The fossil evidence proposed by Martynov (1924), Tillyard (1932) and Carpenter (1943a, 1943b) interpreted the neuropteran venation as having an anterior media. This branch, although arising from the posterior media, fuses basally with the radial sector. It continues as part of the radial sector where it subsequently emerges as an independent apical vein.

On the basis of the interpretation of Coleoptera sharing a common pattern with that of Megaloptera, there is the inclusion of anterior media as part of the apical venation, even though the proximal connection of MA to Rs as occurs in Megaloptera is absent.

Media (M)—This vein emerges proximally from the radius. In the Adephaga this vein is complete, while in the Polyphaga the proximal segment has atrophied as paralleled in the Lemmatophoridae and Sialidae (fig. 4, 32, 36).

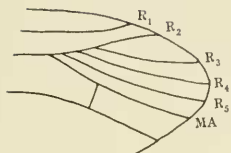
Forbes, although recognizing the fact that a tracheal branch enters the proximal stem (labeled M_{3+4} in fig. 6-7) of cell 10 (i.e. oblong cell by previous authors) of the Cupedidae and Adephaga (fig. 35), chose to regard this as not of any consequence on the assumption that it would not work out to any logical interpretation of the marginal veins. Thus he considered this a medio-cubital cross-vein and not a branch of media.

However, if the condition in *Sialis mohri* Ross (fig. 36) is examined the pattern is seen to consist of an unbranched M_{1+2} with M_{3+4} fusing with cubitus. The fusion of M_{3+4} results in a medial cross-vein appearing distally and aligning itself with an anterior r-m cross-vein.

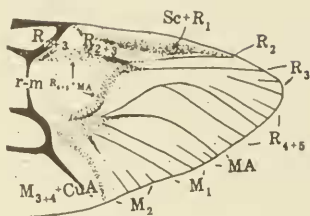
In comparing the Sialidae to the Cupedidae-Adephaga (fig. 6-18) it becomes evident that the condition of the fusion of M_{3+4} and the medial cross-vein pattern form the proximal and distal sides respectively of cell 10 (fig. 6, 35). The upper portion of the cell consists of the branch M_{1+2} . The branch of M_{1+2} forks distally, a portion of which joins to the medial cross-vein and completes the pattern.

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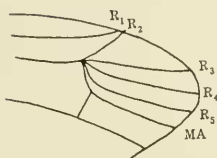
Fig. 21, Cupedidae-Adephaga comparative apical pattern; Series 1. 22, Cupedidae-Adephaga comparative apical pattern; Series 2. 23, Cupedidae-Adephaga comparative apical pattern; Series 3. 24, Cupedidae-Adephaga comparative apical pattern; Series 4. 25, Directional wing pattern. 26, *Hydrophilus triangularis* (Say) (Hydrophilidae); apical venation. 27, Polyphaga comparative apical pattern; Series 1. 28, Polyphaga comparative apical pattern; Series 2. 29, Polyphaga comparative apical pattern; Series 3. 30, *Telephorus* sp. (Lamprophoridae). Folding pattern. After Forbes, 1926.



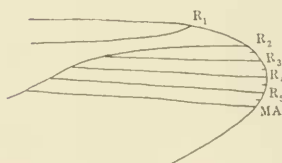
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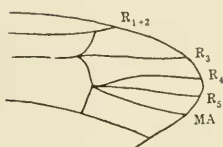
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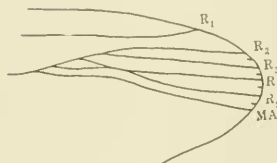
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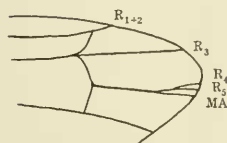
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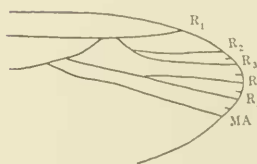
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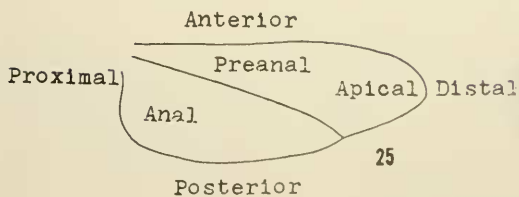
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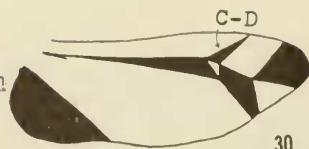
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Much of the branching pattern of posterior media in the Coleoptera has as its parallel a condition found in the Corydalidae (fig. 37). This pattern consists of a branching of M_{1+2} , accompanied by a fusion of M_{3+4} . In Coleoptera, the single appearing M_{3+4} vein subsequently fuses with anterior cubitus as paralleled in the Sialidae (fig. 36). In addition to the Sialidae serving as a parallel pattern in interpreting the nature of media in the Cupedidae-Adephaga, there also emerges a parallel medial pattern in the Lepidoptera (fig. 38). This pattern in conjunction with the Sialidae is considered instrumental in constructing a medial pattern common to both the Cupedidae-Adephaga and Polyphaga specializations. In the Lepidoptera only M_4 is considered fused with CuA_1 . In the Polyphaga there is the same fusion of M_{3+4} with CuA as in the Adephaga but in contrast to the Adephaga, there is the atrophy rather than the fusion of the proximal portion of M_{1+2} . Even though the nature of the fusion of M_2 may differ in Lepidoptera, as compared to the Coleoptera (fig. 38-39), the fact remains that Lepidoptera possesses the parallel specialization involving the fusion of M_2 to M_{3+4} with the subsequent fusion of this series to the branch CuA_1 . M_2 is separate in the Hydrophilidae and partially fused with M_{3+4} in Scarabaeidae (fig. 39).

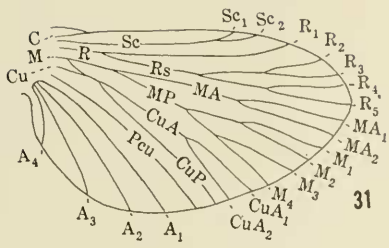
In some of the polyphagan families such as the Bostrichidae (fig. 40), an apical vein emerges from the distal side of the cross-vein. This in turn has been encountered on the proximal side of the cross-vein in the Chrysomeloidea (fig. 42). As a result of a comparison to the Lepidoptera, it becomes evident that the proximal spurious condition as noted in some Chrysomeloidea is the result of atrophy of a portion of the basal segment of M_{1+2} .

Thus the characteristic appearing cross-vein in the Polyphaga which connects the Rs to M is interpreted as consisting of an alignment of a r-m cross-vein to the proximal segment of M_2 . In turn M_2 fuses with $M_{3+4} + CuA$. The distal spur of Chrysomeloidea and the vein in the Bostrichidae is therefore M_1 .

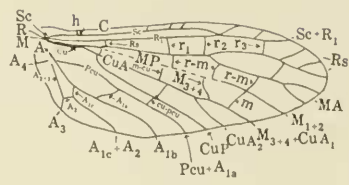
Anterior Cubitus (CuA)—Several recent workers including Martynova (1952), Edmunds and Traver (1954), Adams (1958), and Carpenter (1966) recognize the investigations of Lameere (1922) involving the convex and concave nature of venation, as having

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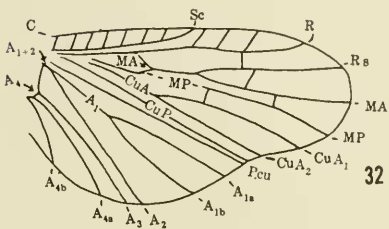
Fig. 31, Hypothetical archetype venation; (modified from Snodgrass, 1935). 32, *Lemmatophora typica* Sellards (Protorthoptera; Lemmatophoridae); after Adams, 1958. 33, Sialidae cellular pattern. 34, Comparative coleopterous cellular pattern. 35, Cupedidae-Adephaga comparative cellular pattern. 36, *Sialis mohri* Ross (Megaloptera; Sialidae); after Adams, 1958. 37, *Protohermes davidi* Weele (Megaloptera; Corydalidae). 38, *Prionoxystus robiniae* Peck (Cossidae). 39, *Canthos probus* (Germ.) (Scarabaeidae); distal branching of M and CuA . 40, *Dinapate wrighti* Horn (Bostrichidae); after Forbes, 1922.



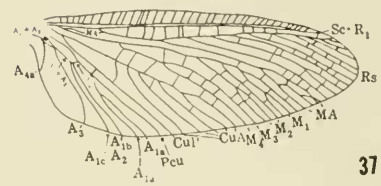
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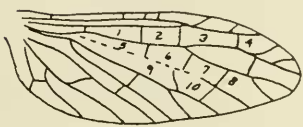
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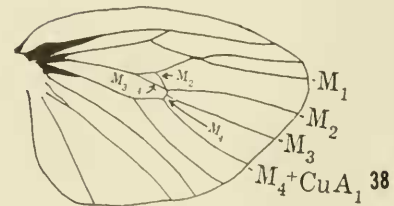
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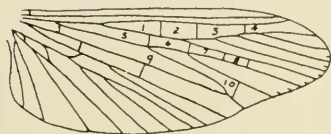
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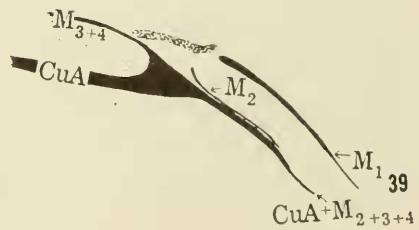
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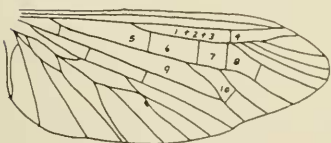
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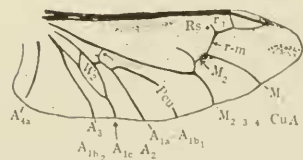
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comparative value in determining the homology of the principal veins. As interpreted by Forbes, cubitus is a strongly convex vein in Coleoptera and appears as a single distinctive vein, dividing the wing into the designated preanal and anal regions. It is in keeping with the nomenclature established by Lameere that this strongly convex vein of the Coleoptera in comparison to the Megaloptera, as well as the accumulated fossil evidence, be designated as CuA (i.e. Cu₁ by other authors). It is further recognized as paralleled in the hind wing of some Ephemeroptera (i.e. *Triplosoba pulchella* (Brongiart), Edmunds and Traver, 1954) that CuA occurs as a single convex vein. In regard to Megaloptera and Lemmatophoridae, this vein in its simplest pattern branches at the apex. As to whether this condition was branched originally in Coleoptera with the subsequent loss of this branching by atrophy or fusion or whether it was originally a single vein is uncertain. Following the above interpretation, account must be made for the loss of posterior cubitus (CuP, i.e. Cu₂ by other authors). There exists in the order Lepidoptera (fig. 43) a parallel specialization in which there is an emphasis placed on the atrophy of this vein. In addition Tillyard (1932) pointed out the atrophy of this vein in the fossil wing *Martynovia insignis* Till. of the family Sialidae (fig. 44). Therefore in order to establish a basis of nomenclature consistent with a paleoentomological and comparative morphological approach, the terms CuA and CuP are tentatively accepted. As recognized by Carpenter (1966), additional histological investigations are needed in order to determine the developmental nature of convex and concave venation in the Endopterygota.

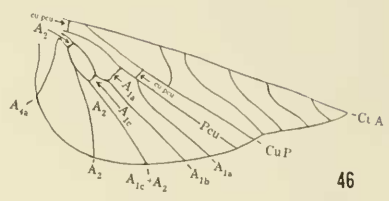
Postcubitus (Pcu)—The vein designated as postcubitus follows the terminology proposed by Snodgrass (1935, fig. 31). This vein is the first anal of Forbes (1922). The recognition of this vein by Snodgrass (1935) as having the status of an independent vein is clearly seen in the fossil family Lemmatophoridae (fig. 4, 32) and Plecoptera (fig. 45). It is recognized further by Snodgrass (1935) that in the more generalized insects, the postcubitus is associated proximally with

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Fig. 41, *Lema trilincata* (Oliv.) (Chrysomelidae). 42, *Migodus tetropiodes* Faim. (Cerambycidae); after Crowson, 1955. 43, *Synemon* sp. (Lepidoptera; Castniidae); after Tillyard, 1919. 44, *Martynovia insignis* Tillyard (Megaloptera; Corydalidae); after Tillyard, 1932; forewing. 45, *Perla languida* Needham and Claassen (Plecoptera; Perlidae); after Needham and Claassen, 1925. 46, *Corydalis cornutus* L. (Megaloptera; Corydalidae); generalized anal lobe. 47, *Corydalis cornutus* L. (Megaloptera; Corydalidae). 48, *Chauliodes pectinicornis* L. (Megaloptera; Corydalidae); pattern of individual variation in the species. 49, *Corydalis cornutus* L. (Megaloptera; Corydalidae); pattern of individual variation in the species. 50, *Corydalis cornutus* L. (Megaloptera; Corydalidae); pattern of individual variation in the species.



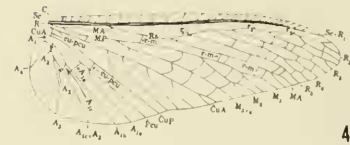
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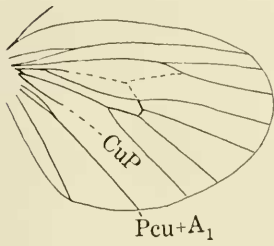
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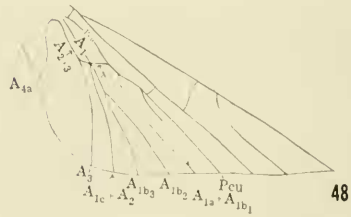
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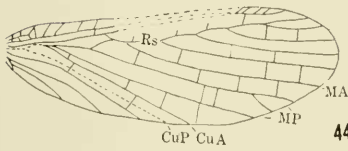
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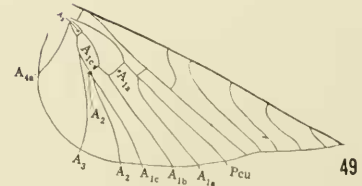
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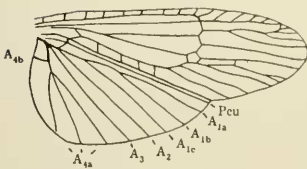
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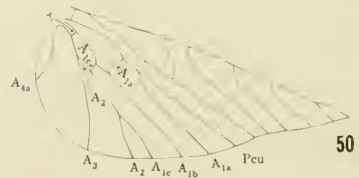
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the cubitus but its base is independent of both cubitus and the anal veins.

In the comparative coleopterous-megalopterous wing pattern, the vein labeled *Pcu* appears to fuse proximally with *CuA*. In the Megaloptera (fig. 46) there occurs a proximal *cu-pcu* cross-vein. In comparison to Coleoptera, there is a possibility of a serial alignment of *Pcu* to that of a proximal *cu-pcu* cross-vein. As to whether there is a direct fusion of *Pcu* with *CuA* or a connection of *Pcu* to *CuA* or a connection of *Pcu* to *CuA* via a *cu-pcu* cross-vein is uncertain.

Anal veins (*A*)—In order to gain a better understanding of the complicated anal venation of Coleoptera, we decided that evidence from a wing outside the order may be instructive. In the selection of such a wing the possession of a well developed anal lobe and venation was important. Such an anal lobe possessing the desirable venation was found in the Corydalidae and the fossil family Lemmatophoridae.

The basic pattern probably has much in common with the modified archetype venation (fig. 31) of Comstock and Needham as illustrated by Snodgrass (1935). The branches of *CuA* have been relabeled to conform to the venational terminology in line with that of the paleontomological interpretations previously discussed.

Using the Lemmatophoridae as a basic pattern (fig. 4, 32), an anal pattern developed consisting of a single anal vein. This pattern further involved a branching of this single vein with the subsequent expansion of this area into a well developed anal lobe.

Thus for the suggested line of development leading to the Coleoptera, the maximum reached was four anals as noted in the archetype, all of which are primary branches of a single vein designated *A*₁, *A*₂, *A*₃ and *A*₄.

Specializations in Coleoptera begin with the addition of venation involving primarily the branching of *A*₁. This condition is noted as having its beginning in a pattern paralleling that of Lemmatophoridae and becoming a parallel part of the specialization trend in such orders as the Plecoptera (fig. 45) and Megaloptera (fig. 47).

The branching pattern of *A*₁ in Coleoptera consists basically of three secondary branches designated *A*_{1a}, *A*_{1b}, and *A*_{1c}. Further specialization resulted in the formation of a tertiary branching of *A*_{1b} (*A*_{1b1}, *A*_{1b2}, and *A*_{1b3}) accompanied by a coalescence of these branches either with each other or with the main branches of the anal pattern. This is based upon studies within the Coleoptera, as well as comparative studies of the Lemmatophoridae, Plecoptera and Megaloptera. From such studies it becomes increasingly evident that the cross-vein appearing pattern in the Coleoptera resulted from coalescence of the longitudinal anal branches.

The following is a comparison between the cross-vein pattern proposed by Forbes (1922) in the construction of his hypothetical wing (fig. 1) and the concept that the anal pattern of present-day Coleoptera originated from a coalescence of the longitudinal anal branches.

1st-2nd cross-vein—As paralleled in the Megaloptera (fig. 46), this cross-vein is a partial fusion of the longitudinal branch of A_{1a} with Pcu . In both the Megaloptera and Coleoptera prior to the fusion of A_{1a} with Pcu , there is a retention of a free proximal segment of A_{1a} . In Coleoptera this pattern is characteristic of both Cupedidae (fig. 6-7) and the Adephaga (fig. 11-17).

1st-2nd a cross-vein—This cross-vein is interpreted as the distal segment of A_{1a} emerging from Pcu as a free branch. In general in the Corydalidae, A_{1a} continues as a free branch to the margin of the wing except as interpreted in the individual species variation in *Chauliodes* (fig. 48).

In the Coleoptera, A_{1a} emerges a short distance as a free branch, after which it fuses, as in the Cupedidae (fig. 6-7), with A_{1b_1} . It then continues as the fused vein $A_{1a} + A_{1b_1}$ to the margin of the wing.

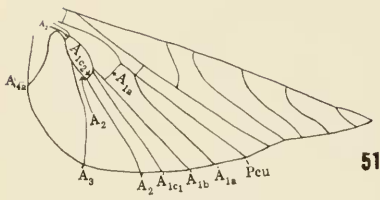
2nd-3rd a proximal cross-vein of the wedge cell (W_1)—As a result of a study of the stages of Corydalidae (fig. 49-50), this condition, as paralleled in the Coleoptera, is the result of a fusion of the branches A_{1c} and A_2 .

Further specialization of these branches is paralleled in the individual species variation occurring in both the Megaloptera (fig. 51-52) and *Priacma serrata* (Lec.) (fig. 53) of the family Cupedidae.

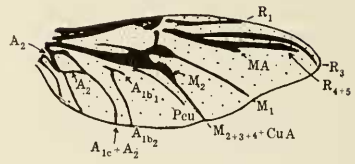
2nd-3rd a distal cross-vein of the wedge cell (W_1)—Forbes based this primarily on the pattern as it appeared in the Cebriionidae, Elateridae, Lampyridae line. As noted particularly in the Lampyridae (fig. 54-55), this is the result of the fusion of the branch A_{1b_3} with the fused vein $A_{1c} + A_2$.

There appears in the Megaloptera (fig. 46) an apparent proximal cross-vein labeled A_2 . From a study conducted on the Scarabaeidae (fig. 56-58), there is evidence that this condition was not originally a cross-vein but rather a proximal fusion for a short distance of A_1 and A_2 (Lemmatophoridae fig. 32) after which A_2 emerges as a free branch and eventually fuses with A_3 . The fusion of A_{2+3} continues for a short distance with the emergence again of A_2 as a free branch. Following this A_2 fuses with A_{1c} .

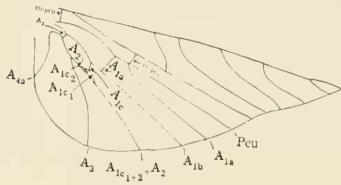
The Coleoptera share with the Megaloptera the possession of a number of preanal cross-veins. Although no one particular coleop-



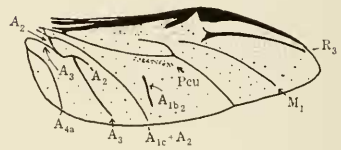
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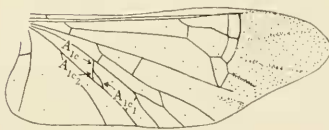
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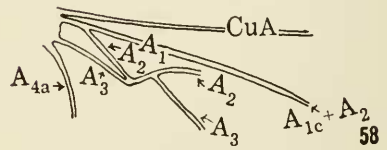
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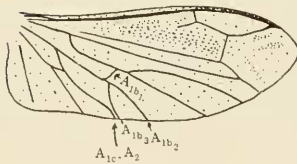
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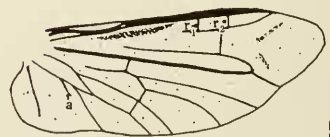
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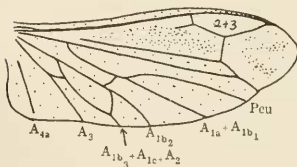
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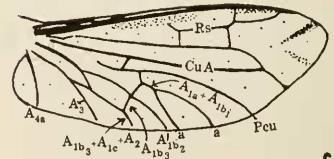
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terous family possesses the number of cross-veins established in the comparative pattern (fig. 2), the number illustrated is basic to interpreting the various cross-veins as they are discussed in relation to family specialization trends.

Cross-veins do vary in number and position. Although they may be treated as comparable cross-veins (i.e. the radial cross-veins), as a result of a parallel drawn between the Megaloptera and the Coleoptera or even certain family parallels within the Coleoptera, it cannot be stated with any certainty that such cross-veins are homologous.

A cross-vein lying proximally between C and Sc is designated as the humeral cross-vein (h) (fig. 6), and is by nature of comparison to the Corydalidae considered as a survival of a once numerous costal-subcostal cross-vein pattern.

Following the interpretation established in relation to the radial branching pattern, the comparative coleopterous-megalopterous pattern consists of at least three radial cross-veins. The first and second radial cross-veins occurring proximal to the C-D fold. This was based largely upon the condition as it occurs in the Polyphaga and particularly that of the Cebriionidae (fig. 59). As discussed previously in relationship to the adephagan radial sector patterns, the third radial cross-vein occurs distal to the C-D fold.

In comparing the Cupedidae-Adephaga to the Polyphaga, there are at least four radio-medial cross-veins. In the Cupedidae-Adephaga pattern the proximal radio-medial cross-vein connects the proximal portion of Rs to M. This cross-vein is believed to have as its counterpart a weakly appearing cross-vein in the Cebriionidae (fig. 60).

There is a prominent radio-medial cross-vein in the Polyphaga which forms the characteristic distal connection between Rs and M. As was discussed in connection with the media, this entire segment is the alignment of the radio-medial cross-vein with the proximal segment of M_2 .

The Cupedidae possess three or possibly four r-m cross-veins, the distal one of which fuses with a proximal segment of $R_{4+5} + MA$ as noted particularly in the Carabidae (fig. 17).

In many coleopterous families, there is an apparent cross-vein

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Fig. 51, *Corydalis cornutus* L. (Megaloptera; Corydalidae); pattern of individual variation in the species. 52, *Corydalis cornutus* L. (Megaloptera; Corydalidae); pattern of individual variation in the species. 53, *Priacma serrata* (Lec.) (Cupedidae); pattern of individual variation in the species. 54, *Photinus pyralis* (L.) (Lampyridae); pattern of individual variation in the species. 55, *Photinus pyralis* (L.) (Lampyridae); generalized pattern. 56, *Pinotus carolinus* (L.) (Scarabaeidae). 57, *Xyloryctes jamaicensis* (Drury) (Scarabaeidae). 58, *Xyloryctes jamaicensis* (Drury) (Scarabaeidae). 59, *Scaptolenus lecontei* (Sallé) (Cebriionidae); pattern of individual variation in the species. 60, *Scaptolenus lecontei* (Sallé) (Cebriionidae); pattern of individual variation in the species.

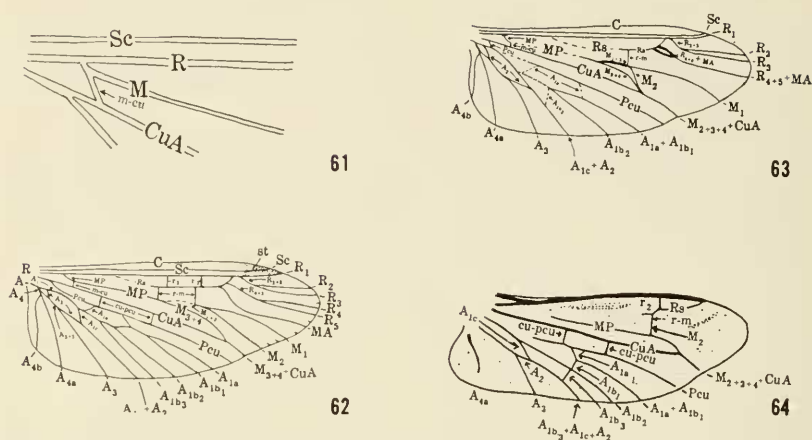


Fig. 61, *Chauliodes pectinicornis* L. (Megaloptera; Corydalidae); proximal relationship of media to radius and anterior cubitus. 62, Polyphaga comparative pattern; Series I. 63, Scarabaeoidea comparative pattern. 64, *Scaptolenus lecontei* (Sallé) (Cabrionidae); pattern of individual variation in the species; after Forbes, 1922.

connecting the radius to the cubitus. This can be traced by comparing *Priacma* (fig. 6) as well as most of the Adephaga to an arrangement noted in such megalopterous forms as *Chauliodes* (fig. 61). This condition involves a fusion of the proximal portion of the longitudinal media with that of a proximal medio-cubital cross-vein. Forbes (1922) in discussing this pattern used the term "arculus" in reference to a similar arrangement which appears in the Odonata.

In a variation of the Sialidae pattern (fig. 36), there is a medial cross-vein which connects M_2 to $M_{3+4} + CuA$. The parallel of this condition forms the distal side of cell 10 of the Cupedidae-Adephaga pattern (fig. 35). In Polyphaga this cross-vein atrophies with the subsequent fusion of M_2 with $M_{3+4} + CuA$ (fig. 62, 63).

In the Megaloptera there are two cross-veins occurring between the cubitus and postcubitus designated as cu-pcu cross-veins. The possibilities involving the relationship of the very proximal emergence of Pcu from CuA have already been discussed. Taking this into consideration, there is present in the Cupedidae-Adephaga (fig. 17-18) and Polyphaga (fig. 64) at least two cu-pcu cross-veins. Of these two, the proximally occurring cu-pcu cross-vein in the Adephaga is often in alignment with the branch A_{1a} . This condition was interpreted by Forbes as an "anal arculus," the composition of which was the proximal portion of the vein designated as 1stA and the 1st-2nd cross-vein. However, King (1956) pointed out in a discussion on

the Dytiscidae, that a portion of *Pcu* (1stA after Forbes) is retained proximal to the alignment of the *cu-pcu* cross-vein and the free branch of *A*_{1a}.

Therefore the approach followed in this investigation considers that the generalized comparative coleopterous-megalopterous pattern is not based upon any one particular wing but is a venational pattern which is shared with the Megaloptera and supported by parallel evidence from the Lepidoptera, Plecoptera, and the fossil family Lemmatophoridae. The selected comparative parallel patterns as exhibited by the orders other than Coleoptera serve as guides in an attempt to determine the path of development along which the present-day coleopterous venation became established.

Following the completion of this paper (unpublished dissertation, 1971) Hamilton (1971, 1972) published a series of papers using a similar type of approach. Ponomarenko (1972) published an account of a single fossil wing of a beetle from the Upper Permian deposits. Both recognize the close affinity of Coleoptera to Megaloptera. It is important to point out that our approach involved an in-depth study of the order Coleoptera and we differ mainly in our interpretation of the anal field of venation.

Because Ponomarenko has illustrated a fossil wing which on the basis of folding is considered to be that of a beetle wing, we believed it important to compare the ideas presented in Ponomarenko's paper to those already discussed. Ponomarenko emphasizes in his discussion the existence of compound veins. In particular he recognizes such possibilities as the anterior branch of *media* merging distally with the posterior branch of the radial sector. Furthermore he points out that as a result of the folding and unfolding of the wing, proximal parts of longitudinal veins may assume the role of former cross-veins and that an independent vein is frequently considered a branch of a completely different vein.

The primary difference between Ponomarenko's proposal and ours is in the interpretation of the anal venation. Therefore the following discussion is a comparison of the two proposals.

The vein labeled by Forbes as 1A is designated by Ponomarenko as a posterior branch of cubitus, *Cu*₂ or *CuP*. In our investigation this vein is postcubitus (*Pcu*) after Snodgrass (1935), the posterior branch of cubitus being lost. The acceptance of this vein as postcubitus (*Pcu*) rather than cubitus posterior (*CuP*) designates it as an independent vein corresponding to that of the Lemmatophoridae. As already emphasized the proposal of this vein as *Pcu* is necessary in making a comparison of the coleopterous pattern to that of Megaloptera. The basis of this comparison is the recognition of fused longitudinal veins in the anal area in place of cross-veins.

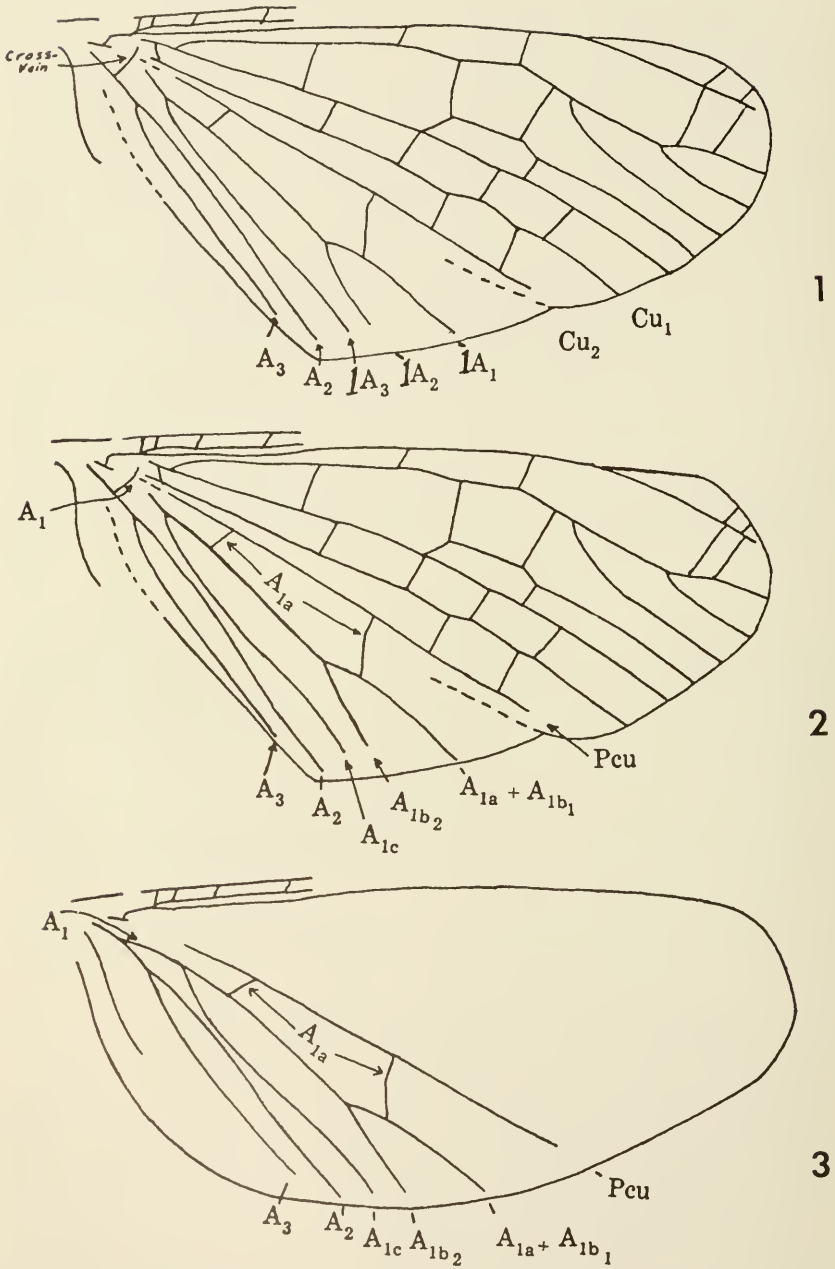


Plate II. 1, Hind wing of a beetle from Upper Permian deposits near the village of Chepanikha (Urals) after A. G. Ponomarenko, 1972. 2, The venational system proposed by Wallace and Fox. 3, The proximal arrangement of A₁ according to Wallace and Fox.

Ponomarenko, in discussing the basal area of the first and second anal veins, indicates the presence of a segment which he states could not be the anal arch as designated by Forbes but is simply a cross-vein. However, this segment would appear to be the broken proximal portion of A_1 . This would be in keeping with the comparative patterns proposed in this investigation. In Plate 2 is illustrated a comparison of the two proposals.

It is significant to point out in the proposal set forth by Ponomarenko that the existence of compound veins, the pectinate nature of the radial sector and the presence of numerous cross-veins except in the anal area, are all in keeping with the present comparative morphological study.

CONCLUSIONS

From venational studies conducted within the order Coleoptera, it is apparent that the generalized pattern of this order exhibits a close affinity to the suborder Megaloptera. It is evident, however, that the coleopterous venation is not derivable from any single present-day venational pattern. Therefore, in order to establish a pattern which can be considered fundamental, other orders such as the Lepidoptera and the fossil family Lemmatophoridae are used in addition to a comparative study of available families within the Coleoptera.

As a result of a comparative study involving the families of Coleoptera, the suborder Megaloptera, and the fossil family Lemmatophoridae, the following is interpreted as fundamental to the comparative coleopterous-megalopterous venational line of development:

1. The preanal venational pattern consists of a costa, subcosta, radius, radial sector, anterior and posterior media, and anterior cubitus. Anterior media was included because of the close affinity the Coleoptera have to the Megaloptera and therefore was considered a remnant of the apical venation in present-day Coleoptera. The ordinal cross-vein pattern is unstable in number and position, the maximum number of which is not present in any single coleopterous family. Due to the stability of 3 radial cross-veins observed throughout most of the Megaloptera, the coleopterous ordinal pattern, originally consisted of 3, 2 of which occurred as a part of the original polyphagan pattern and one in the adepagan pattern. In comparison to the Lemmatophoridae, the coleopterous ordinal pattern is believed to possess originally a marginal thickening designated as the pterostigma.
2. The apical venation was originally pectinate in configuration, the nature of which was altered greatly as a result of folding. As discussed in relationship to the Hydrophilidae, this pattern

- may have consisted originally of a variable amount of accessory branching, a specialization of which is common to many of the Megaloptera.
3. The anal venation consists of a postcubitus vein directly connected to anterior cubitus or indirectly connected by means of a serial cu-peu cross-vein. As is a consistent feature of the Megaloptera, the anterior primary branch of the first anal fuses partially with postcubitus.
 4. The anal venation was originally a single vein from which formed a basic pattern consisting of four primary branches designated A_1 , A_2 , A_3 , and A_4 .
 5. An investigation into the nature of the individual patterns of variation within a megalopterous species as well as certain species of the Coleoptera, reveals that the basic primary branches have undergone secondary branching pattern. The secondary branching pattern established is restricted principally to the primary branch A_1 and to a lesser extent A_4 (a pattern often paralleled in the Plecoptera). A_1 branches three times forming secondary branches designated A_{1a} , A_{1b} and A_{1c} . In turn, as part of the ordinal pattern, a third or tertiary branching had taken place, which was restricted to the secondary branch A_{1b} . To these tertiary branches were given the terms A_{1b_1} , A_{1b_2} , and A_{1b_3} . The primary branch A_4 divides forming secondary branches A_{4a} and A_{4b} .
 6. The line of development leading to the Coleoptera consists of an anal pattern in which there was a lack of any cross-vein development. In place of cross-vein patterns and possibly to add support to this area of the wing, there developed in the Coleoptera a characteristic pattern involving coalescence of anal veins. In many cases this has led to the development of a pattern which appears to possess cross-veins.
 7. Coalescence of the anal branches consists principally of a fusion of A_1 and A_2 proximally for a short distance, after which A_2 emerges as a free branch distally. The anterior secondary branch A_{1a} fuses with Pcu , emerging as a free branch distally. The posterior secondary branch A_{1c} fuses with the distal free branch of A_2 and continues to the margin of the wing.

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